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FACTORS INFLUENCING ODOR SENSITIVITY IN THE DOG

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20. ABSTRACT contd.

train. In contrast, when dogs are sitting alert but not engaged in odor detection, presentation of a novel odor may disrupt the normal breathing pattern only momentarily and the integrated volume shows little change.

CONTENTS

SUMMARY

This report covers an investigation of the possible influence of adaptation on the ability of dogs and human subjects to detect an odor and quantitative measures of flow rate and associated parameters in dogs sniffing odors.

Detection curves were previously derived for alpha-ionone for four German Shepherd dogs. To determine the generality of those findings, six men and one woman were tested in the same apparatus using comparable procedures and the same compound. Human detection curves reach their asymptotes in one and half log units of concentration while those of dogs extend over five log units. The marked discontinuity in the slope of the canine detection curves was also seen in the curves for four of the human subjects and in one case extends over 50% of the dynamic range. Three subjects showed no discontinuity.

Human thresholds for alpha-ionone fell at a mean concentration of 4.5×10^{9} molecules/cm^{3} while canine thresholds were at 4.5×10^{5} molecules/cm^{3}.

The possibility that the above findings may have been influenced by adaptation was investigated by three approaches: estimation of exposure time to odor during trials; analysis of frequency of errors following a correct response; examination of the affect of varying intertrial intervals from 30 to 90 sec on correct performance. None of these investigations yielded evidence that adaptation has any significant affect on performance under the conditions of the present study.

A technique has been developed for the quantitative analysis of the relation between odor detection task and sniff parameters. Thirsty dogs are rewarded with water for identifying which of two ports is associated with an odor. Sniff flow rate, frequency and amplitude are recorded from the output of a pneumotachometer behind one port. When dogs are engaged in an odor detection task the normal pattern of respiration is interrupted and replaced by trains of rapid sniffs usually structured around 1-3 trains consisting of 3-7 sniffs per train. Flow rates during individual sniffs range over 16-87 l/min. Peak flows, however, are sustained less than 0.5 secs. Volumes range from 5-220 cc/sniff and durations from 25-163 msec. Sniff frequencies are about 6-7.5/sec. In contrast, when dogs are sitting alert but not engaged in an odor detection task presentation of a novel odor may disrupt the normal breathing pattern only momentarily and the integrated volume shows little significant change. Presentation of an odor to which the dog had previously been trained to respond did disrupt the normal pattern more significantly although only during the course of the first second of odor presentation.

A. ODOR DETECTION PERFORMANCE IN DOG AND MAN

Introduction

Previous reports have outlined investigations of odor detection performance in 4 German shepherds and six human subjects. These results demonstrated discontinuities in the slopes of the stimulus-response curves for alpha-ionone, provided evidence of the dog's superior detection abilities and stressed the importance of individual differences in performance. Data from three of the six human subjects are shown in Fig. 1.

There is a possible criticism of these findings, however, which was not covered by control experiments. It concerns adaptation. In psychophysical studies of human subjects it is a general finding that sensitivity to an odor is reduced following prolonged exposure to high concentrations of the same odor. But at least one worker (KÜster) has also reported adaptation effects for brief presentations at relatively low concentrations. The time available for recovery from possible adaptation effects in such studies can be measured by the duration of the intertrial interval. In the present studies intertrial intervals were about 30 seconds. (However, the time spent sampling the presentation bays is also a factor in considering adaptation effects and this was considerably longer for human subjects than for dogs.) Is it possible that the level of performance of dogs and men are depressed if the intertrial interval does not reach a certain magnitude greater than 30 secs? If so the true thresholds might be lower than those we reported, and anomalies in stimulus-response curves might reflect altering degrees of response depression by adaptation.

To examine these possibilities we used three approaches: (1) observation of the dogs behaviour during trials. The frequency and duration of odor sampling should be significant factors influencing adaptation. These, however, are under the dogs control. (2) Systematic variation of intertrial intervals. (3) Analysis of previously obtained records to determine whether the probability of an error occurring was greater following a correct than an incorrect response.

Methods

The apparatus and methods used for testing both canine and human subjects were outlined in previous reports. In brief, thirsty dogs are trained in a programmed odor-choice apparatus to sample each of three odor-air presentation days and indicate (by the sustained interruption of a photocell beam) which of three bays is associated with an odor. If a correct choice is made the dog is rewarded with water delivered to a cup inside the bay. If incorrect, access to the bay is blocked. Each bay receives odor filtered air from an air-dilution olfactometer.

Human subjects were tested in the same apparatus using basically the same procedures but rewarded with 10¢ each time a correct choice was made. In addition the subjects sniffed through a teflon-covered cone one end of

which was placed over the outlet of the vapor diffusion disc in the test bay. They were allowed to sniff in any way and for as long as they chose. However, in the case of three subjects, each timed the duration of the sampling period with a stopwatch. (The sampling period was defined as the time elapsing between the opening of the bay doors and the making of a choice. It did not include the intertrial interval.)

The behavior of dogs during trials was observed through the one-way glass panels at the front of the presentation bays. We recorded both the movement patterns and the time spent sniffing for trial blocks selected at random from various test sessions (involving different concentrations of alpha-ionone).

To assess the influence of varying intertrial intervals one dog was tested over a minimum of 100 trials on each of the following intertrial intervals: 30, 45, 60 and 90 secs, while two human subjects were tested on 30 and 90 sec intervals. The test odorant was α-ionone delivered at a concentration of $10^{-4.5}$ (for human subjects) and $10^{-5.5}$ for dogs (α-ionone was also used in the main series of trials).

Results

(a) Sampling duration during trials: assessment of exposure time to odors

All dogs were highly consistent both in patterns of approach and sampling from the bays, and in average sniffing times for odor and blank air. While at very low concentrations dogs showed up twice the number of discrete samplings from each bay, measured sniffing times for each sampling showed little variation. Sniffing times for odor and blank air, respectively, averaged 1.04 and .98 secs based on 10-trial blocks selected randomly from general sessions. This observation agrees with sniffing times observed in experiments involving a two-choice apparatus and pneumatochograph (see below).

With the exception of the lowest concentrations stimulus exposure due to active sampling rarely exceeded a total of 5 secs. This would be accumulated, for example, by four or five one-second sniffs, each separated by one or two seconds of sampling blank air. With the requirement that an animal keep its snout in a bay for five seconds to signal choice of that bay, an additional four seconds of potential odor exposure must be considered. And finally a period of five seconds is allowed for consuming water from a bay.

Further exposure to the odor is possible during drinking. The average drinking time for two dogs observed over several sessions were about the same: 3-4 seconds. A conservative estimate for the maximum total adaptation time would thus be about 12 seconds per trial; the actual time of exposure to odor can safely be considered less than 12 secs since neither active sniffing nor inspiration during normal breathing occurs continuously throughout this interval.

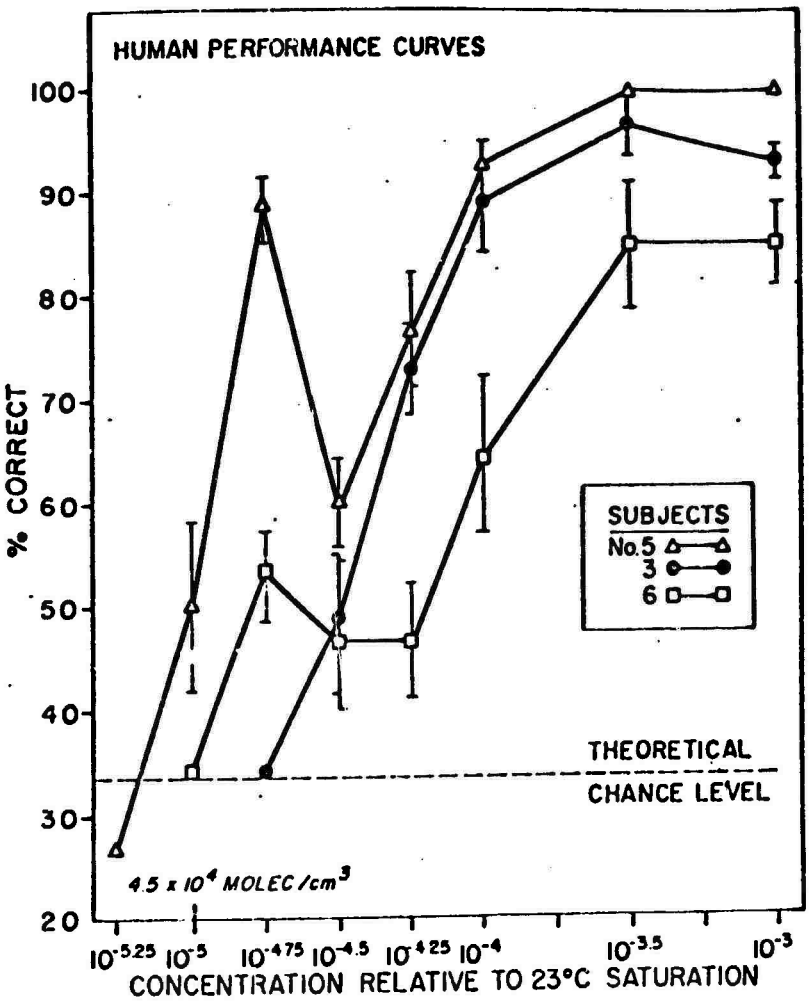

Fig. 1 Detection curves for α-ionone in three male human subjects ($4.5. \times 10^9$ moles/cm^3 refers to the mean detection threshold). Each point on the curve is the mean ($\pm$ SE) of at least 150 replications.

The standard intertrial interval used was 30 seconds. Thus the average de-adaptation time, counting trials with minimum or no sampling, ranged from 30 secs (error-free performance) to several minutes after a succession of errors. Since de-adaptation time is at least twice the maximum interval during which adaptation might have occurred, we would expect from the usual time course of adaptation-recovery curves that any effects within the data would not be large. (A further related point supports this view: considering performances of all but the poorest subject, an overall average of 94 per cent during second series testing was maintained over concentrations 10^{-3} to 10^{-7}. This represents nearly three-fourths of the total range and strongly suggests that any adaptation effects occurring at higher concentrations were small.)

Human subjects varied from a few seconds to several minutes in the time they spent sampling bays before reaching a choice. At higher concentrations sampling was generally rapid. Near threshold, however, subjects would occasionally take up to 4-5 mins.

To determine whether longer sampling time was associated with a changed level of performance, correlation coefficients were calculated between mean sampling time and mean performance scores of all subjects for each concentration. The results show that no significant correlations exist. Thus there is no evidence that adaptation effects appear when exposure to the odorant is prolonged.

(b) Analysis of sequence of correct and incorrect responses

Session records of trials run in the main series of experiments (that established the detection curve for alpha-ionone) were analyzed to determine whether there were significantly more errors following the initial exposure to an odorant in a block of trials. The data chosen for analysis were the first five trials in each of the final ten sessions for Dogs No. 1 and 4 (the best and worst performers respectively). This was repeated for each test concentration.

Results of this analysis appear in Table 1. The data are given in 2 x 2 contingency tables showing frequencies of occurrence for combinations of correct ("1") responses and errors ("0"). Values of chi-squared with associated probabilities are given for several of the lower concentrations in A., and for each of the four sets of contingencies in B. It can be seen that the combination of correct response following a correct response occurs with a frequency significantly greater than that of other combinations. The two instances where this is not true are at 10^{-7} and 10^{-8} in A.; in these cases, no combinations occur significantly more often than others. Among the four combinations, the frequencies of an error following a correct response are generally the lowest. We therefore find no evidence of adaptation effects in the occurrence of errors following correct responses. Further examination of response sequences beyond the fifth trial revealed no instances of repeated error runs separated by one or two correct responses, nor alternating patterns of correct and incorrect responses.

Table 1. Analysis of response sequences for Dogs 1 and 4: Correct ("1") versus error ("0") responses using last 10 sessions per concentration.

A. First trial paired against second trial.

10^{-3}

	1	0
1	10/10	0/0
0	0/0	0/0

10^{-4}

	1	0
1	10/9	0/1
0	0/0	0/0

10^{-5}

	1	0
1	10/8	0/1
0	0/1	0/0

10^{-6}

	1	0
1	7/8	0/0
0	3/2	0/0

First Trial \ Second Trial	Dog 1/Dog4	

χ^2= -/4.4; p = -/<.05

10^{-7}

	1	0
1	2/3	1/2
0	3/3	4/2

χ^2= 0/.42; p = .99/.5

10^{-8}

	1	0
1	2/1	2/2
0	4/4	2/3

χ^2= 1.4/1.9; p = .3/.2

B. Sequential pairings of adjacent trials based on total data for 7 test concentrations, 10^{-3} through 10^{-9}.

First Trial \ Second Trial	1	0
1	42/39	5/7
0	15/14	8/10

χ^2= 4.5/4.7; p = <.05/<.05

Second Trial \ Third Trial	1	0
1	48/42	9/10
0	9/6	4/12

χ^2= 7.4/11.9; p = <.01/<.001

Third Trial \ Fourth Trial	1	0
1	51/38	6/10
0	7/8	6/14

χ^2= 7.1/10.4; p = <.01/<.005

Fourth Trial \ Fifth Trial	1	0
1	57/36	1/11
0	6/9	6/15

χ^2= 20.7/8.7; p = <.001/<.01

While runs of several errors are seen in some records, these are generally infrequent except for concentrations at or below threshold where chance-level performance occurs.

(c) Variation of intertrial interval

The effects of increasing intertrial intervals on the performance of one dog and two human subjects are summarized in Table 2. The maximum score was 100. If adaptation had been acting to depress performance at the minimum time interval a higher score should be obtained at longer intertrial intervals. The mean values for 30 sec and for increased intertrial intervals in both dog (A) and human (B) subjects show that this did not occur. The effects are very slight: probabilities of the outcomes in A and B (Table II) being $p = 0.42$ and $p = 0.29$ respectively (Mann-Whitney U-test). Furthermore they are in the opposite direction from that expected if adaptation were occurring.

Conclusion

The evidence from these studies and analyses clearly indicates that the duration of the intertrial interval (30 secs) used in the main series of experiments (on both dogs and human subjects) was not too brief to allow recovery from any adaptation to the test odorant that might have occurred.

Table 2. Comparisons of session scores for standard and increased length inter-trial-intervals.[1]

A. Data from Dog 4 at a concentration of $10^{-5.5}$.

Standard (30 sec.) ITI	Increased inter-trial intervals	
100	96	45 sec.
88	97	
96	92	60 sec.
98	90	
91	93	75 sec.
$\bar{X}$ = 94.6	$\bar{X}$ = 93.6	

B. Data from two human subjects at a concentration of $10^{-4.5}$.

Standard (30 sec.) ITI	ITI increased to 90 sec.
80	87
100	80
70	73
80	73
47	50
67	80
67	47
80	80
$\bar{X}$ = 73.9	$\bar{X}$ = 71.3

[1] Performance scores are given as percentages based on 50-trial sessions.

II. RATES, AMPLITUDES AND PATTERNS OF AIR AND ODOR FLOW DURING SNIFFING IN DOGS

1) Measurement of sniff parameters in dogs perf ning an odor detection task

Introduction

Several lines of evidence point to the need for an accurate quantatitive analysis of the characteristics of sniff cycles when an animal is actively engaged in an odor detection task. No such analysis has been made in any animal including man except in relation to isolated measures of sniff volume (1-3 l/mm in man: D. Laing, personal communication, 1975) and sniff frequencies in rats (1-11 cycles/sec). These studies, however, provide no accurate information about the detailed composition of the sniff cycle or the extent to which it varies with concentration (particularly at low dilutions). We have therefore sought to provide such information for a dog performing a learned odor detection task. A dog was trained to respond differentially to the presence of an odor in such a way that it sniffs through a pneumotachometer. The ultimate aim is not only to measure accurately the flow amplitude, duration and frequency but also to determine whether these parameters vary as a function of concentration, nature of the odor and of the task (i.e., whether it is odor discrimination or detection). If the mode of dispersal of odors within the olfactory organ is important (for example, in discrimination rather than detection) it should be reflected in such data. Since the work is still in progress and data have not yet been analyzed this is a preliminary report.

Methods

Subjects

Two female and one male German Shepherd were used. One female was about three years old at the start of the experiments while the other dogs were about one year old. They were housed in temperature controlled indoor runways, fed laboratory chow ad lib, and placed on a 23-hour water deprivation schedule. During testing and training they received an average of about 400-600 cc of water as rewards. The difference between this quantity and 1500 cc was given to them early each morning following the day of testing.

Behavioral test apparatus

The apparatus provides two bays, one associated with the odor of amyl acetate, and the other a blank. The two bays are set in a wooden console. Two swinging metal doors carry the sniffing ports. They are counterweighted to allow the dog to push them open but can be latched in position to block the dog's access to the water bowls (visible beneath the doors). The experimenter releases the latch by remote control when the dog makes a correct choice. The bowls are gravity fed from calibrated water reservoirs in the upper section of the console.

Behind each sniffing port are two metal cylinders of similar length and diameter extended inwards by polyethylene cylinder. One of these is the Fleish pneumotachograph, the other is a dummy. To equalize flow resistance in the two cylinders the internal lumen of the dummy is fitted with a smaller cylinder. Since their relative positions can provide no differential cues, the cylinders occupy the same positions permanently. The cylinders are open at both ends but near the opening into the interior of the console there is a port on the floor of each polyethylene cylinder. This is made to accommodate a 10 cc vial, set so that its mouth is flush with the lumen of the cylinder. A loose glass wool plug about 3 cc in volume is placed into each vial. 25 drops of pentyl acetate in the diluent (ethylene glycol) are delivered to one vial and 25 drops of the diluent alone are delivered to the other. The sample vials are recharged after several runs are made to ensure reliable stimulus production. The relative positions of the vials (test and "blank") are varied according to a randomly determined sequence. Between trials each chamber was flushed out with a fan to ensure that no odor would remain to interfere with the next trial.

Each of the sniffing ports is surrounded with a ring of foam rubber. This allows the dog to insert its snout into the port without irritation yet seals tightly enough to prevent air leaking around the dog's snout.

Odorant and concentration determination

N-pentyl acetate was chosen as the first odorant because it has previously been used in olfactory studies (on rats, rabbits, tortoises, pigeons and man) involving both electrophysiological and behavioral apparatus; has a sharp distinctive odor with a known trigeminal threshold lying well above the olfactory threshold and has no known biological significance for the dog. It was diluted with ethylene glycol (Baker reagent grade) to the appropriate concentration.

Since the odor in the cup is being diluted with the air drawn into the nosecone, the dog experiences a stimulus concentration considerably less than that present in the sample cup headspace. In order to estimate this dilution effect, a sample cup of saturated amyl acetate was put in place, air was drawn through the chamber as in sniffing, and then a sample was withdrawn from the chamber by gas-tight syringe and injected into the gas chromatograph (GC). Comparison of GC peak areas of these samples with equal volume samples of saturated amyl acetate vapor from the bottle headspace revealed that a dilution of about 1000 to 1 was being made from sample cup to pneumotach nosecone.

To avoid any confusion stemming from these differences we will refer to concentration in solution as % concentration and concentration in air as a fraction of vapor concentration (10^{-3}, 10^{-4}, etc.).

Recording apparatus

The pneumotachograph is a device that measures flow rates with high accuracy and minimal resistance. The flow resistor elements are a large number of ducts (each 0.8 mm in diameter and 32 mm long) packed into a brass tube. When air is drawn through the outer layer of ducts the difference in pressure at two ports (separated from each other along the long axis of the tube) is used to measure flow. This pressure difference is translated into an electric signal by means of differential pressure transducer. (This has a strain gauge as one arm of a wheatstone bridge.) The signal from the pressure transducer is amplified and displayed on a pen recorder and oscilloscope or recorded on tape for later display.

To calibrate the pneumotachograph for volume a 1000 cc syringe was fitted with an adaptor to attach it to the pneumotachograph, and air drawn through into the syringe. The amplitude of the pen deflection was then plotted against flow rate. To calibrate for flow rate flowmeters were used. Temperatures were relatively constant during trials and the volume of tidal air involved was small (in the order of 100 cc).

Training and testing

The procedures for training and testing were based on principles outlined in earlier reports. In essence, the dogs were required to respond differentially to the presence of the odor by pushing on the appropriate door with their snout. A novel feature, however, was the need to train dogs to insert their snouts into sniffing ports. Initially they were required to keep their snouts in the ports for 1-3 seconds. However, when this task was learned (and the dogs were responding differentially to the presence of the odor) they were allowed to set their own time since this was one of the variables under study.

Training began at concentrations of 10% until performance stabilized at 90% or more correct responses. The concentration was then lowered to 1% and the process repeated. The final concentration used for testing was .01% (corresponding to approximately 10^{-6} of vapor saturation).

Dogs sniffed into the port associated with the pneumotochograph both when the odor was present and when the diluent alone was present. Consequently the time required to make a correct choice could be identified.

Results

Dogs readily learned to sniff into the ports. While they were able to maintain this position for 1-3 seconds during training, all required considerably less time to make a choice when allowed to take as little or as much time as they required. This parameter showed much individual variability, however.

When a dog first inserted its snout into the port the pneumotachometer recordings showed an immediate downward deflection which probably represents the displacement of air through the pneumotachometer by the snout rather than expiration of air.

Data for one dog show that sniffing bouts are usually structured around 1-3 trains with 3-7 sniffs per train. Occasionally one or two isolated sniffs may occur following the main train but the initial train invariably contains less than three sniffs.

Examples of data derived from responses to both air and odor are given in Table 3 and Fig. 2. (In interpreting this data it should be borne in mind that the dog may sniff first from either the right port which is always associated with the pneumotachometer or the left port. Thus the initial train recorded may or may not be the initial train of a trial. Secondly, the dog may sample the left port between trains recorded here as a single bout. For the purposes of compiling this data a single sniff was counted whenever the trace fell below baseline.)

There is an insufficient number of responses to allow firm generalizations but there is some indication both here and in other records that the largest volume sniff occurs towards the end of a train - usually the 1st or penultimate sniff. Furthermore, sniffing trains generally begin rather tentatively with one or more low volume sniffs. Beyond these features and the tendency for frequencies to occur between 6.0-7.5/sec. there is little uniformity in the sniff pattern. Even the frequency figures are misleading in so far as they imply regular spacing of sniff cycles. Individual sniffs (inhalations) are separated by varying periods of exhalation or of minor fluctuations around the baseline and the durations of the sniffs themselves are highly variable.

Flow rates during individual sniffs range from 16-87 l/min. Peak flows, however, are only reached momentarily (<5 m sec duration). In one case, however, a flow rate of 50-56 l/min was sustained for 60 m sec. Volumes range from 5-220 cc/sniff and durations from 25-163 m sec. A sniff train varies from 0.438-1.138 secs. of which actual sniffing (inhalation) seldom accounts for much more than 1/2.

While it is too early to interpret this data in terms of the pattern of dispersion of odorants at olfactory surface, it is interesting to observe the frequency with which individual sniffs achieve their peaks - or decline from them - by a series of secondary peaks. This "jitter" should increase turbulence and thus may act in directing eddy currents into the more remote recesses of the olfactory chamber.

There is some indication that the dog spends longer (per unit volume sniffed) in investigating an odor associated than an air related port. For example, in Table 3 the ratio of Total Volume sniffed/total duration of trains is 0.35 for odor as against 0.45 for air. The time spent actually sniffing air and odor (per unit volume sniffed) is, however, similar. (The corresponding ratio is 0.85 for odor as against 0.83 for air.)

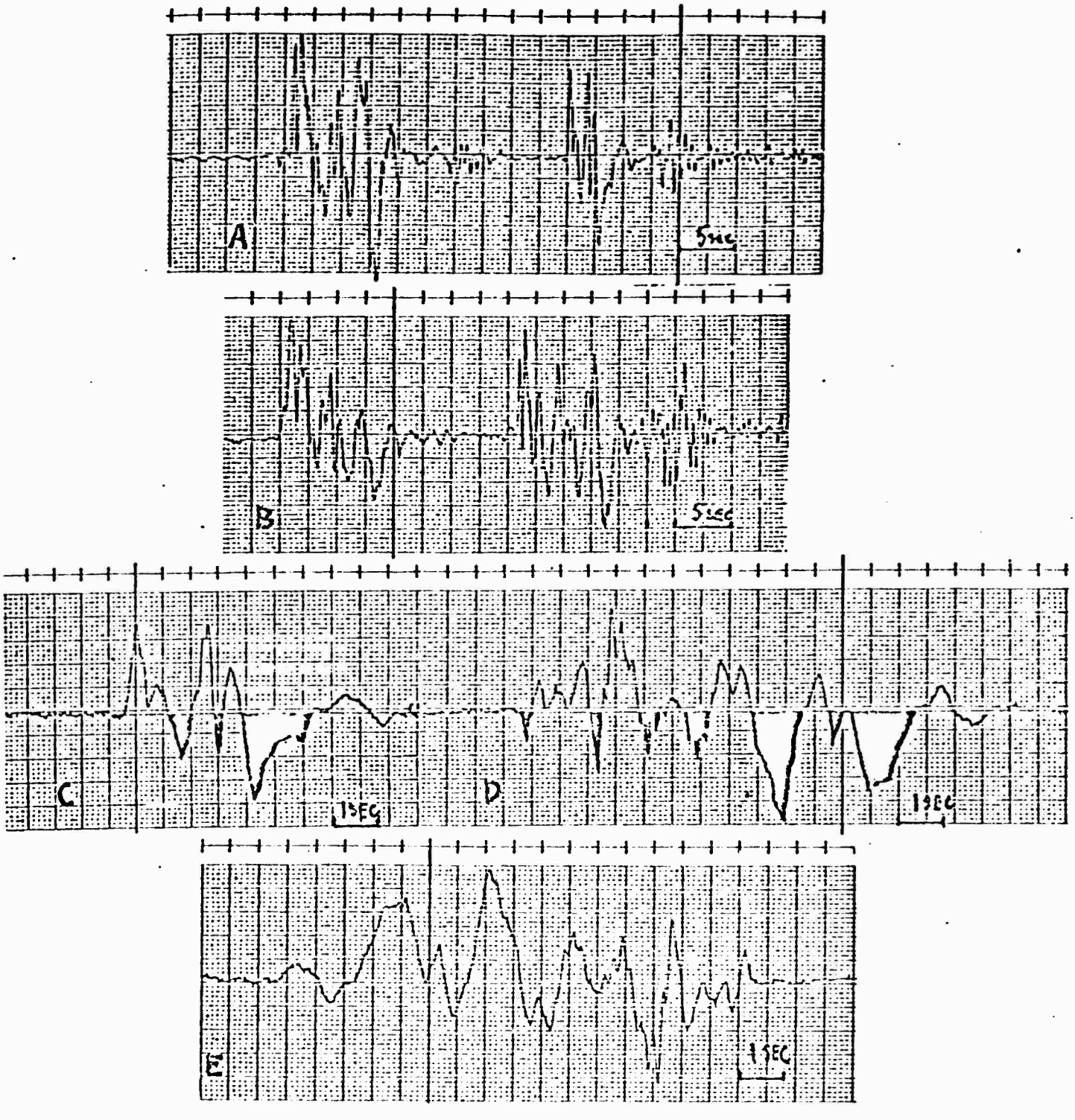

Fig. 2. Pneumotachograms of sniffing trains.

SNIFF TRAIN	TOTAL* DURATION (m. sec)	NUMBER OF SNIFFS IN TRAIN	FLOW RATE (l/min)	VOL. (cc)	DURATION (m. sec)	FREQUENCY (per sec)
1 AIR	975	1	22.0	10	38	6.1
		2	44.0	31	31	
		3	31.5	19	50	
		4	34.5	30	63	
		5	77.5	150	113	
		6	56.0	165	150	
2A ODOR	800	1	21.5	10	25	7.5
		2	44	63	100	
		3	16	5	25	
		4	44	75	100	
		5	87	220	163	
		6	31	40	63	
2B ODOR	500	1	34.5	30	56	6.0
		2	28	15	25	
		3	61	133	156	
3 AIR	438	1	16	10	35	6.8
		2	37.5	40	46	
		3	56	83	100	
4A ODOR		1	23	15	38	3.5
		2	31.5	58	103	
		3	59.5	160	153	
		4	59.5	53	150	
4B ODOR		1	79	140	125	
		2	56	95	125	
4C ODOR		1	68.5	185	150	

Table 3. Flow rate, volume and durations of sniffs drawn from over 0.1 per cent of amyl acetate in polypropylene glycol ("odor") and the diluent alone ("air").

*Total duration refers to elapsed time between start and finish of sniff train and includes exhalation as well as inhalation (sniff) time.

2) Measurement of sniff parameters in dogs not performing a learned odor detection task

Introduction and methods

The data reported in the previous section was derived from dogs trained to detect odors. To provide some basis for comparison, however, it is important to know what differences occur in the responses of dogs that are not actively engaged in a learned task. We therefore ran a further series of trials with dogs resting in a laboratory and breathing air at a relatively normal rate. Two of the three compounds tested were odors to which the animal had not previously been exposed. The compounds were α-ionone (which the dogs had been trained to detect); valeric acid and cineole.

Flow rate was measured with a Fleisch pneumotachograph attached by way of a specially-constructed aluminum cone (padded on the internal surfaces) and face mask. The dog had been habituated to wearing this device. The odors were held under the pneumotachograph in open neck bottles for approximately 1.5-2.0 seconds.

In addition direct measures of flow rate, "averaged" or "integrated" records of flow volume were obtained.

Results and Discussion

Examples of traces are shown in Figs. 3-6. In Figure 3 the dog is inspiring room air at a relatively normal rate (approximately one per second). Despite the erratic flow rate trace it is clear from the integrated readings that volume exchange is relatively constant and the breathing pattern stable.

In Figs. 4 and 5 an odor (to which the dog had not previously been exposed) was placed beneath the pneumotachometer intake. The preceding trace (not shown) indicated that until just before the marker indicating stimulus delivery was activated the animal was breathing normally. It is clear that the pattern of normal inspiration is interrupted in a very similar manner in both cases. However the integrated volume shows that the interruptions have little influence on the total volume exchanges (cf. Fg. 3). In contrast, the responses shown in Fig. 6 are to alpha-ionone - a compound to which this dog had been trained to respond in the three choice apparatus. In this case the interruption of the trace is more pronounced although it persists for less than one second (successive traces were normal).

These findings suggest that the casual sniffing of odors by the dog is a different phenomenon from the sniffing that occurs when dogs are actively seeking an odor source. They are more transient and may significantly influence volume exchange only when the odor is one to which the animal has been trained to respond or has otherwise acquired biological significance for the dog.

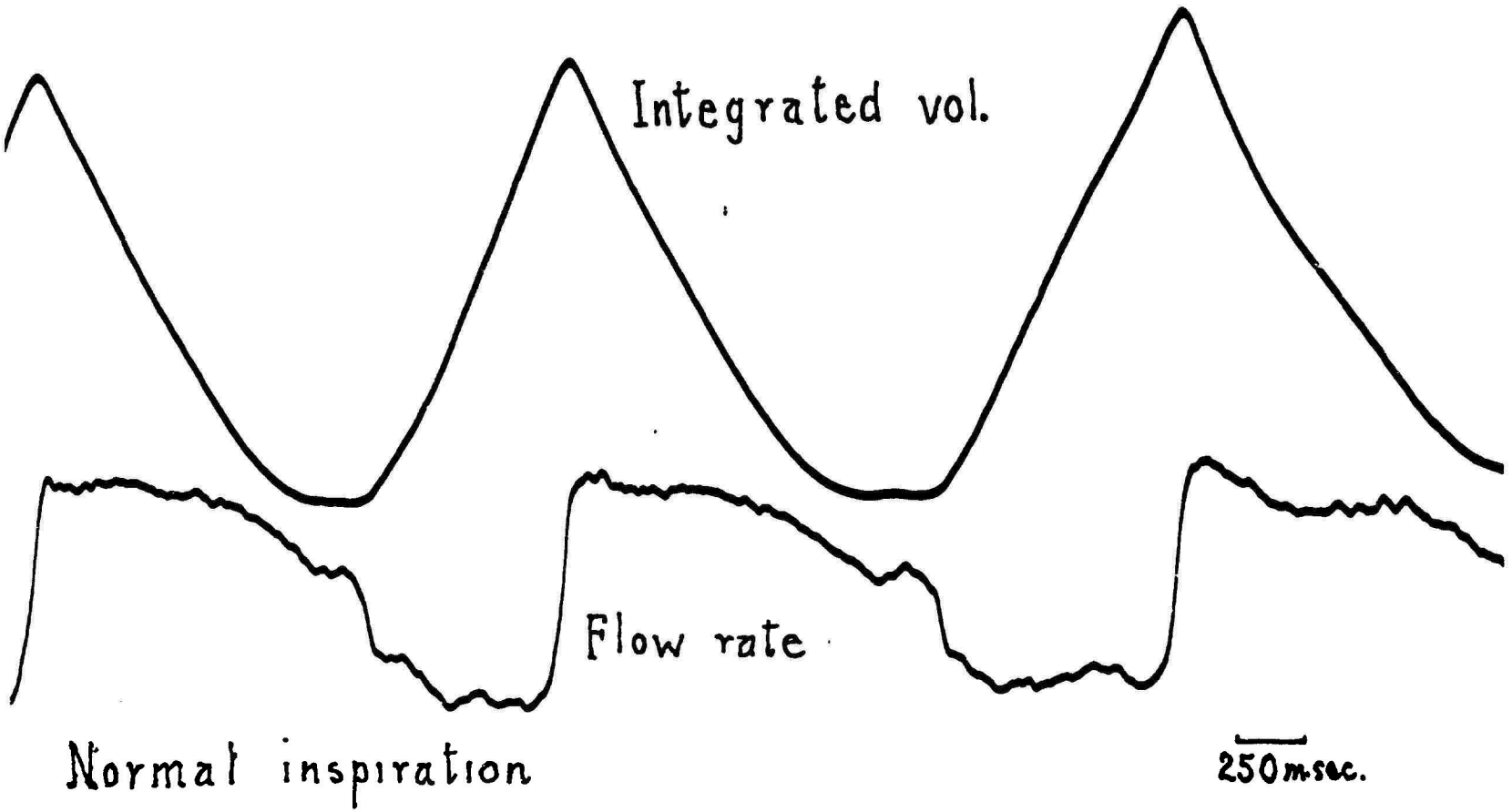

Fig. 3. Comparison of integrated volume and flow rate of air movements of dog (R) respiring room air between test stumuli. Downward deflections represant inhalation.

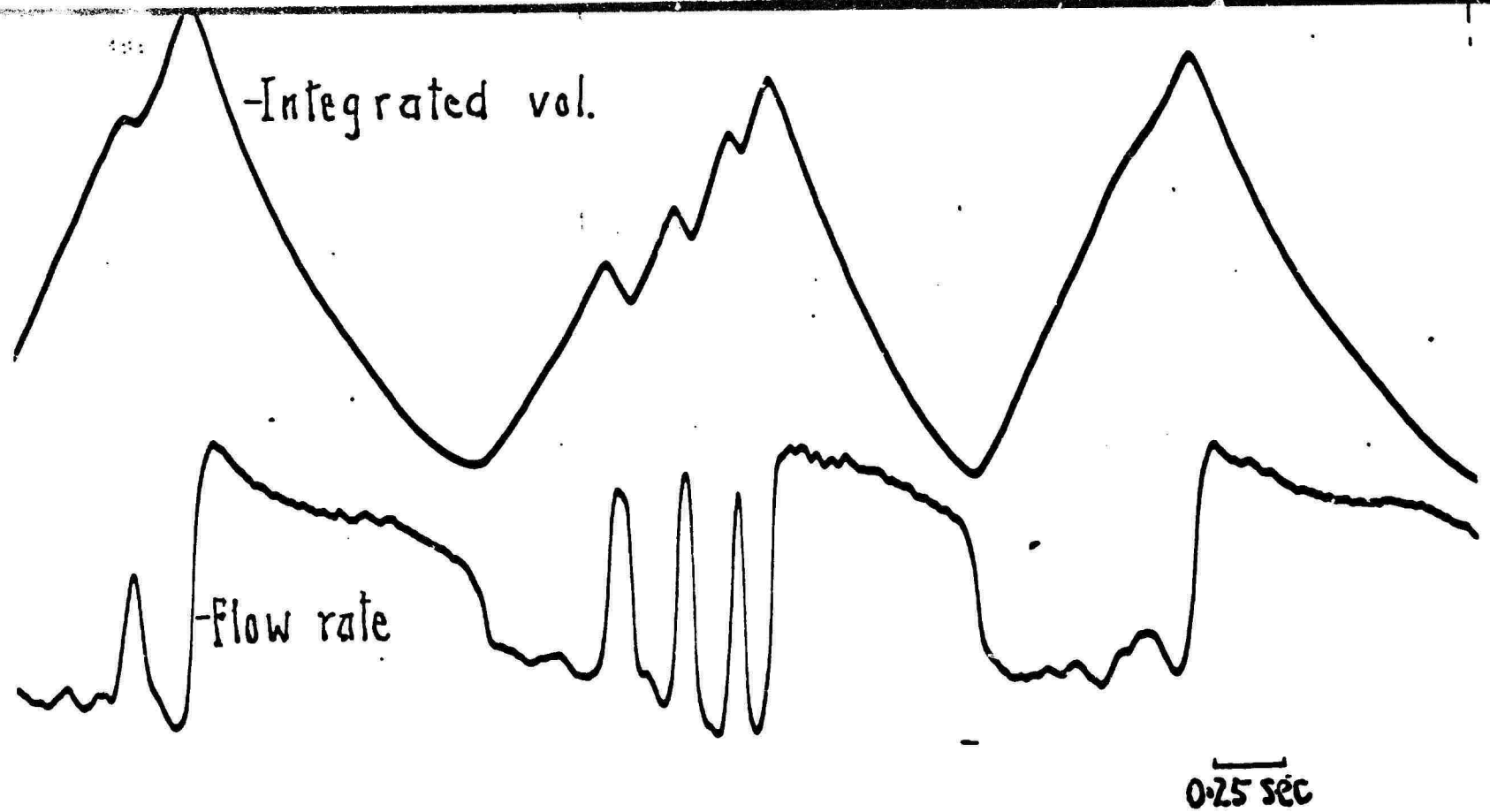

Fig. 4. Integrated sniff volume and flow rate of air movements of dog(R) sniffing valeric acid. Downward deflections of upper traces represent inhalation. Upward deflection of lower trace indicates stimulus delivery period.

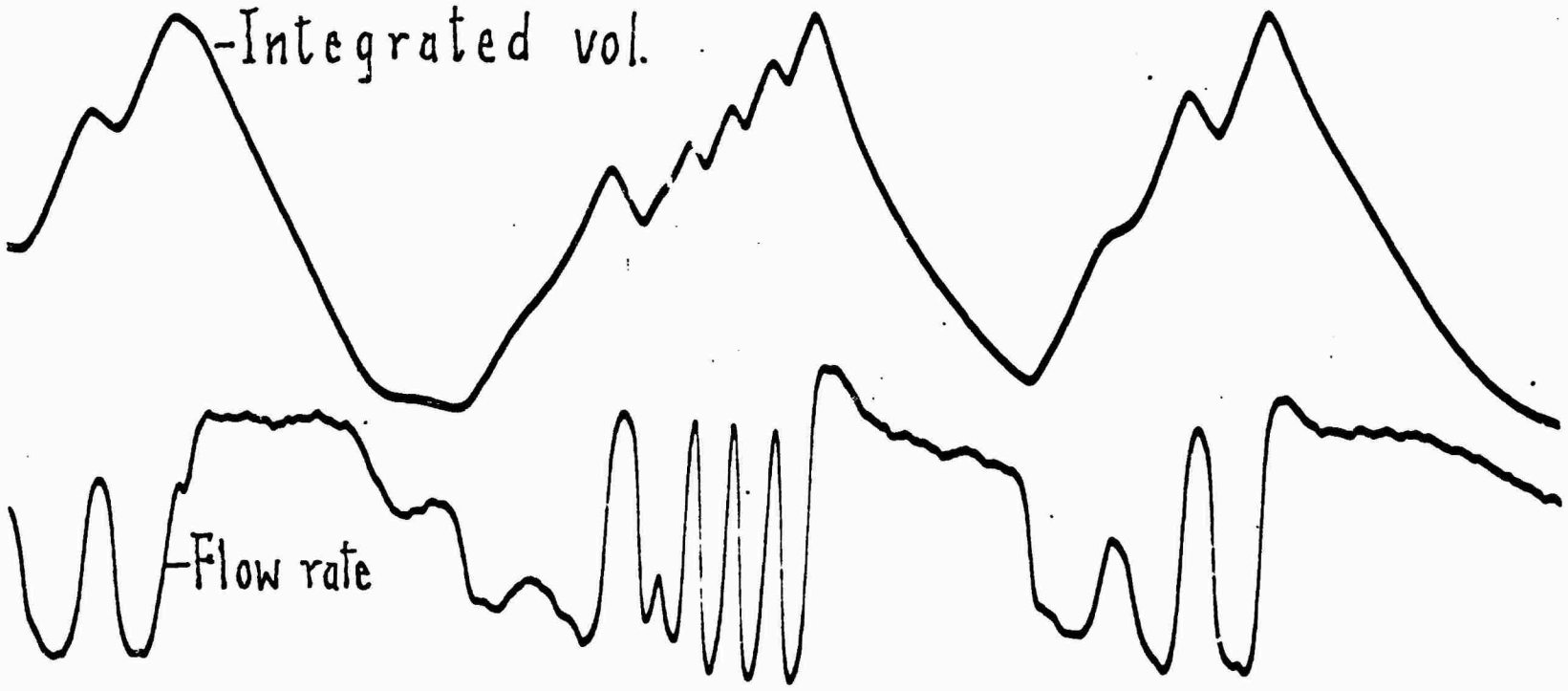

Fig. 5. Integrate sniff volume and flow rate of air movements of dog (R). Sniffingcireole
Downward movements represent inhalation. (Same time scale as previous figures.)
Upward deflection of lower trace indicates stimulus delivery period.

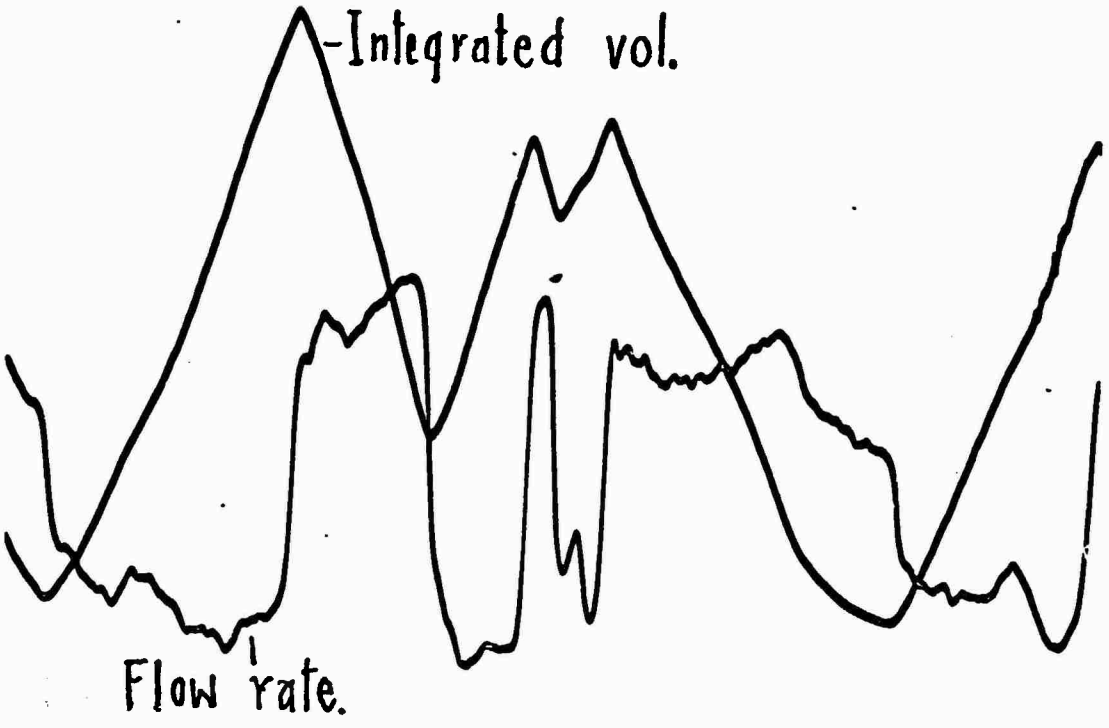

Fig. 6. Integrated sniff volume and flow rate of air movements of dog (R) sniffing α-ionone. Downward movements represent inhalation. (Same time scales as previous figures.)

PUBLICATIONS RESULTING FROM THIS GRANT

Pietras, R. J. and Moulton, D. G. (1974) Hormonal influences on odor detection in rats: changes associated with the estrous cycle, pseudo-pregnancy, ovariectomy, and administration of testosterone propionate. Physiol. and Beh. 12, 475-491. (Monograph)

Kauer, J. S. (1974) Response patterns of amphibian olfactory bulb neurones to odor stimulation. J. Physiol. (Lond.), 243, 695-715.

Kauer, J. S. and Moulton, D. G. (1974) Response patterns of olfactory bulb neurones using odor stimulation of small nasal areas in the salamander. J. Physiol. (Lond.), 243, 717-737.

Pietras, R. J. and Moulton, D. G. (1975) Influences of gonadal steroids on an odor detection task in the rat. In: Denton, D. (editor), Olfaction and Taste V. New York: Academic Press (in press).

PRESENTATIONS GIVEN ON WORK RESULTING FROM THIS GRANT

Moulton, D. G. (1974) Odor detection in dog and man. Paper given at the 1st Congress of the European Chemosensory Research Organization. Orsay, France, July 4th.

Moulton, D. G. (1974) Influences of gonadal steroids on an odor detection task in the rat. Paper given at the 5th International Symposium on Olfaction and Taste. Melbourne, Australia, October.